

LIFE HISTORY AND PREDATOR-PREY INTERACTIONS OF THE NEMERTEAN *PARANEMERTES PEREGRINA* COE

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This study concerns the life history of the predatory nemertean *Paranemertes peregrina* Coe, predator-prey relations of *P. peregrina*, testing of predator strategy models, and a consideration of the effects *P. peregrina* has on community structure. *P. peregrina* occurs from Eisenada, Mexico through the Aleutian and Commander Islands (Coe, 1940), and also in Japan (Yamaoka, 1940). It lives in both muddy bays and rocky intertidal areas, and eats polychaetes (Roe, 1970).

Nemerteans are common in intertidal areas of temperate regions. Most are carnivorous (Coe, 1943) and, because of their size and abundance, may be important organisms in marine communities. No complete investigation of the feeding ecology of a free-living nemertean has been done, and since the great majority of nemerteans are free-living, such a study should add greatly to the knowledge of the phylum.

MATERIALS AND METHODS

Three study areas were chosen: two mud flats on San Juan Island, Washington, and the ballast along the ferry landing at Edmonds, Washington.

The study site at Snug Harbor, Mitchell Bay (48° 34' 9.5" N, 123° 9' 48" W), San Juan Island included the area between -0.2 m and -0.4 m, where *P. peregrina* was common. (A tidal height of 0 equals mean lower low water, as recorded in the U. S. Coast and Geodetic Survey Tide Tables.) The fauna contained mainly polychaetes, tanaids, and thalassinids, plus much ulvoid algal cover most of the year. Only the superficially dwelling polychaetes, with certain exceptions, were available as prey for *P. peregrina*, and included the nereid *Platynereis bicanaliculata*, the hesionid *Ophiodromus pugettensis*, the opheliid *Armandia brevis*, the spionid *Scolecopsis fuliginosa*, syllids, polynoids, and phyllodocids. Polychaetes living in deep tubes included the nereid *Nereis vaxillosa*, lumbrinerids, terebellids, maldanids, glycerids, nephtyids, ariciids, and dorvilleids.

The study area at Garrison Bay (48° 34' 57" N, 123° 9' 17" W), San Juan Island, Washington, extended from -0.1 to -0.5 m. Polychaetes and many clams comprised the major infauna and algae were much less common here. Polychaetes included the superficially dwelling *P. bicanaliculata*, *A. brevis*, *O. pugettensis*, syllids, at least five species of spionids, and phyllodocids; plus deeper dwelling *N. vaxillosa*, lumbrinerids, terebellids, maldanids, glycerids, cirratulids, ariciids, sabellids, and oweniids. *Aglaia diomedea* (cephalaspid gastropod), common at both

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mud flats, attained high densities in summer and overwintered as juveniles just below the mud surface.

The study area at Edmonds, Washington, ($47^{\circ} 48' 12''$ N, $122^{\circ} 22' 56''$ W) consisted of boulders 1.5 to less than 0.3 m high, piled along the north face of a ferry landing. Tide level was from +2.1 m at the top of the highest rock to about +0.2 m at the top of the lowest. Boulders were covered with a thick coat of *Balanus cariosus* and *Mytilus edulis*. Syllids (*Typosyllis* sp.) were most common in clumps of larger barnacles, and mussels and spionids (*Boccardia* sp.) were most abundant in cracks between small barnacles. Other polychaetes included phyllodocids, lumbrinerids, the chrysopetalid *Palcanotus chrysoplepis*, polynoids, and very few nereids.

In Washington lower low tides between September and January occur during hours of darkness; those from April through July occur during daylight hours. February, March and August have both daylight and nighttime lower low tides. Most field work was carried out during lower low tidal periods from April, 1968 through August, 1970.

Densities of active *P. peregrina* were determined by counting numbers/m² in randomly selected (or all) square meters along transects on the substratum surface during the time of maximum nemertean activity (within an hour after the tide recedes). Transects were chosen haphazardly with respect to nemertean densities. If few worms were active, all worms seen were counted and collected. Each month the numbers/m² of active nemerteans in each of five permanently marked 10×4 m² mud flat areas were counted to get density measures through time in given places.

In alternate months four $\frac{1}{4}$ m² mud samples from each mud flat were dug, the numbers of *P. peregrina* on the surface were counted, then all nemerteans in sieved mud were counted to determine total density. The per cent of active worms was determined by dividing the number on the mud surface by the total number. Since sieving mud was so time consuming, not enough samples were taken to get statistically significant results.

For size-frequency studies, the first 50–100 worms were collected from the density transects each month. In the laboratory their length and width were measured after allowing each worm to extend to its normal crawling length; their sex was determined by observing gametes through the ivory colored venter.

To determine what *P. peregrina* had been eating, another 50 worms (also along the density transects) were collected each month. After being brought to the laboratory, these worms were immediately isolated into small jars, half full, of clean sea water, and after 48 hours were measured, sexes were determined, and faeces were identified and preserved in 70% alcohol. Faeces of *P. peregrina* are easily identified bundles of polychaete setae and jaws in mucus.

Nemerteans used for measurement and faecal analysis were returned within a few days to approximately the places within the study areas from which they were collected. Areas were cleared of *P. peregrina* to study movement and total densities. To measure growth and movements, individuals dyed with neutral red (making the white ventral streak pink) were put into permanently marked areas. Every month the number of marked worms still in or near the given square meter were counted,

collected and measured, and returned to the same m^2 . The ventral streak remained pink for at least eight months.

Population densities of the major prey, *Platynereis bicanaliculata*, were determined during alternate months at Snug Harbor and Garrison Bay. Mud was collected into numbered jars (20 cm^2 surface area at opening) or plastic freezer containers (surface area 100 cm^2) at regular intervals throughout the study area. In the laboratory, the contents of the containers were emptied with sea water into a pyrex dish and agitated until all nereids swam to the surface of the water. They were counted and collected, and nereids from the samples with the most nereids were preserved in 70% alcohol. The preserved nereids were later measured for size frequency analysis.

Other prey species' densities were determined as follows: specimens of *Armandia* and spionids were counted in most of the nereid samples. Very few spionids were seen in these samples, so in August, 1970, all the spionid tubes seen per 1/100 m^2 while diving at high tide at Snug Harbor were counted. *Nereis virens* densities were estimated from the numbers collected in $\frac{1}{8}$ m^2 mud samples taken for total *P. peregrina* counts. At Edmonds, barnacles and mussels were scraped off small patches of rock, and in the laboratory the volumes of the clumps were determined, and they were broken apart and the polychaetes found were counted.

To determine activity periods of *P. peregrina* dives using S.C.U.B.A. equipment were made at each study area, day and night, and at all tides except lower low tide to see if, and how many, nemerteans were active other than when uncovered at lower low tides. The dispersion pattern of *P. peregrina* was determined by the method described by Pielou (1959), using the formula $\pi D^2 w = a$.

During several low tides the behavior of the animals was observed, especially with respect to foraging, feeding, time required to feed, and movements. For behavioral observations artificial mud flats were made in shallow concrete outdoor aquaria. The aquaria were about 1 m^2 in size, and each contained a wooden frame about 5 cm smaller per side than the aquarium. Water came through hoses above the aquaria, and a plug at the bottom of each aquarium outside the wooden frame could be pulled for "low tides." Because of the inner frame, water had to percolate through the mud while the mud flat was draining; it did not simply run off the surface of the mud. Nemerteans responded as if there was a real low tide when water was thus forced down through the mud on its way out. The activity cycles of individual nemerteans were observed in these small mud flats.

Two similar indoor mud flats were also made and kept going for ten months. One contained nereid food for the nemerteans but no "low tides" were made, to determine if *P. peregrina* would eat under water. The other contained no nereid food and was established to determine how long specimens of *P. peregrina* can withstand starvation. In both experiments, running sea water was used, and no data were collected to determine if nemerteans absorbed dissolved food from the water itself. Nemerteans from each flat were removed once each month, measured, weighed, and then returned. Jaws of nereids that were consumed in the natural habitat of *P. peregrina* were collected from the faeces and measured using a calibrated compound microscope.

Laboratory feeding experiments were done in two ways. First, adult nemerteans do not feed very well if simply left in a container with prey; prey must be placed

directly in front of a nemertean's head before it is recognized as prey. Each day adults were presented with as many nereids as they would eat and results were recorded. Secondly, young nemerteans will eat if enough nereids are included in the container to be detected. For a year three juvenile nemerteans were grown in pint jars with nereids in a refrigerator kept near 7° C and the number of nereids eaten was recorded.

Diversity of prey species was calculated as $H' = -(n_i/N) \ln (n_i/N)$ (Pielou, 1966). Significant differences in H' were determined by the method of Pielou (1966).

Dietary selectivity was calculated by applying Ivlev's (1961) "electivity coefficient." This coefficient, E , is a ratio of the amount that a food type is eaten to its abundance or availability, $E = (r_i - p_i)/(r_i + p_i)$.

OBSERVATIONS AND RESULTS

Population life history of P. peregrina

Lengths of *P. peregrina* are correlated with dry weight ($r = 0.77$, $P < 0.001$), but length \times width (area, mm²) is more highly correlated with dry weight ($r = 0.93$, $P < 0.001$) and this index is the size unit used throughout. Linear regression of length \times width on dry weight is: area = 2.11 dry weight + 50.33. Figure 1A and B gives sizes of *P. peregrina* through time at Garrison Bay. Roe (1971) shows sizes of individuals through time at Snug Harbor and Edmonds and sizes of Garrison Bay individuals during other months.

Gamete production. The presence of developing eggs and sperm can be determined 3-4 months before the gametes are ripe. In all three populations the total number of females significantly outnumbered the total number of males: Snug Harbor, 452 females, 196 males, $\chi^2 = 101.1$, $P < 0.005$; Garrison Bay, 105 females, 52 males, $\chi^2 = 17.9$, $P < 0.005$; Edmonds, 147 females, 29 males, $\chi^2 = 79.1$, $P < 0.005$. Even during the peak spawning seasons females outnumber males about two to one (Fig. 2; see Roe, 1971 for more detail). At Snug Harbor and Garrison Bay part of the population consists of non-ripe animals at peak spawning periods also (Fig. 2; Roe, 1971).

Spawning. The major spawning season for all three populations is spring or summer, and minor spawning periods occur throughout fall and winter in the mud flat populations (Fig. 2 for Snug Harbor; Roe, 1971, for Garrison Bay and Edmonds populations). At Garrison Bay the major spawning period is in April, and a few worms spawn in November (Roe, 1971). At Snug Harbor most spawning occurs in June, with some also in November (Fig. 2); and at Edmonds spawning occurs in March and April only (Roe, 1971). The major spawning season for each population usually lasts about a month; spawning is not highly synchronous within a population; and the dispersion pattern of *P. peregrina* is random during spawning season.

Eggs and sperm are shed through temporary gonopores along the dorsolateral surfaces of adults. In the laboratory, spawning sometimes resulted in death of the adult. Adults kept after spawning lived for six weeks and then died from poor laboratory conditions.

Coe (1940, p. 286) said, "gelatinous clusters containing many ova (are) deposited during the warmer months of the year," by *P. peregrina*. Although spawn-

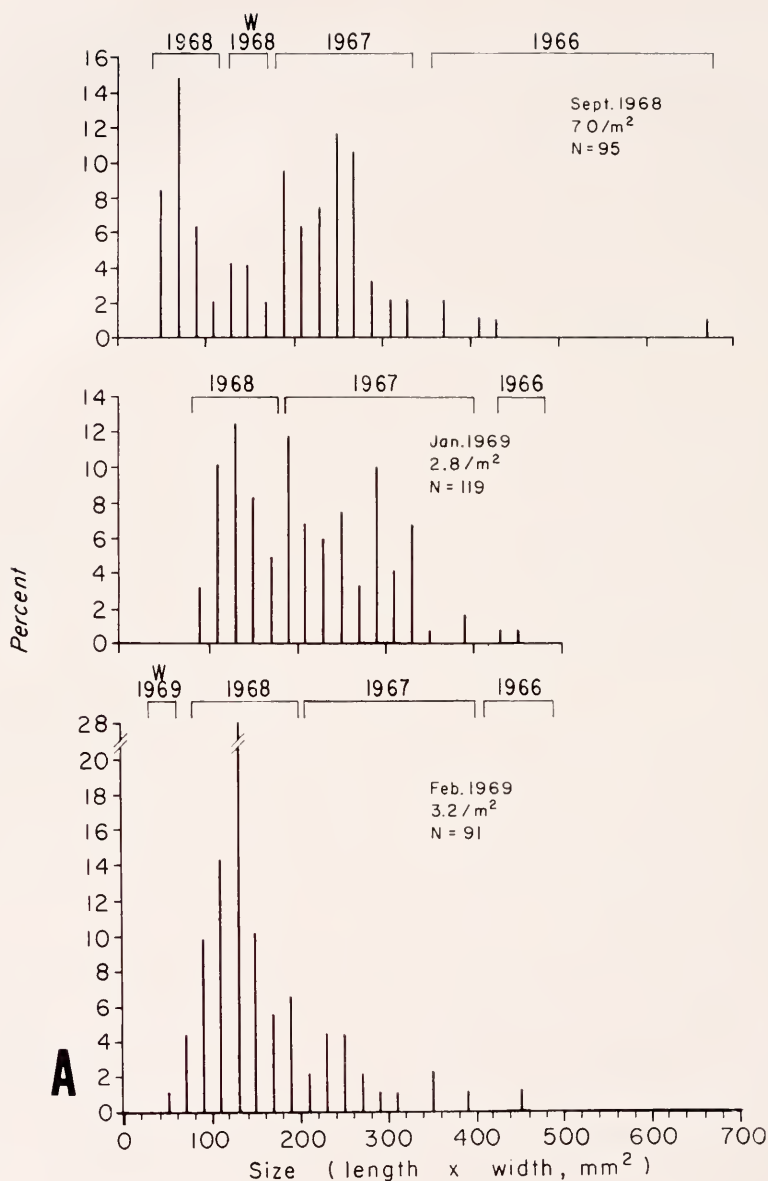
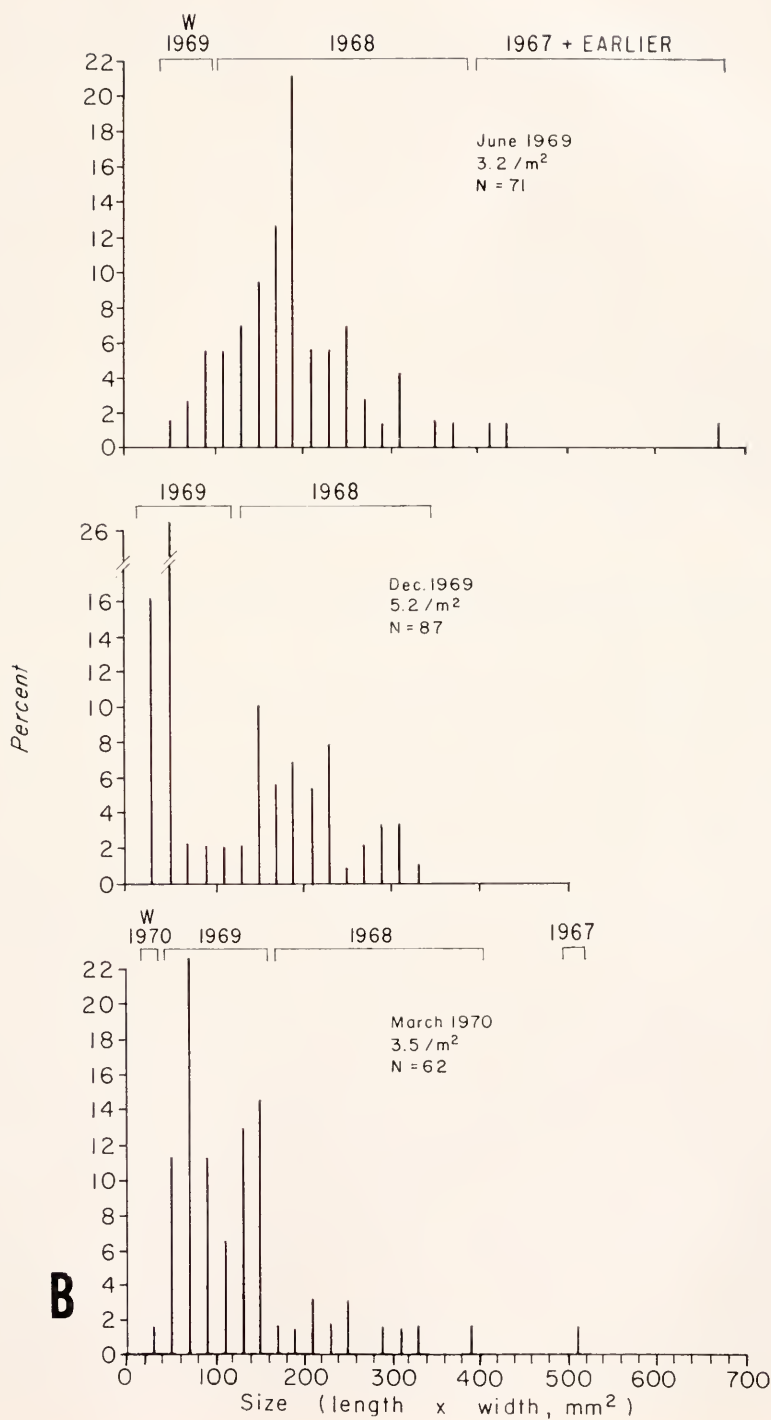


FIGURE 1. A) Size-frequency distribution of *Paranemertes peregrina* at Garrison Bay, September 1968, January 1969, and February 1969. Size class interval is 20 mm². Number/m² is the average total *P. peregrina* density. N is the number in the sample from which the size-frequency histogram was drawn. W equals winter recruits. B) Size-frequency distribution of *Paranemertes peregrina* at Garrison Bay is continued; June 1969, December 1969, and March 1970. Number/m² for June 1969 is the average *P. peregrina* density during low tide. The December 1969 sample includes an area of unusually high density of juveniles, thus increasing the percent in small size categories.



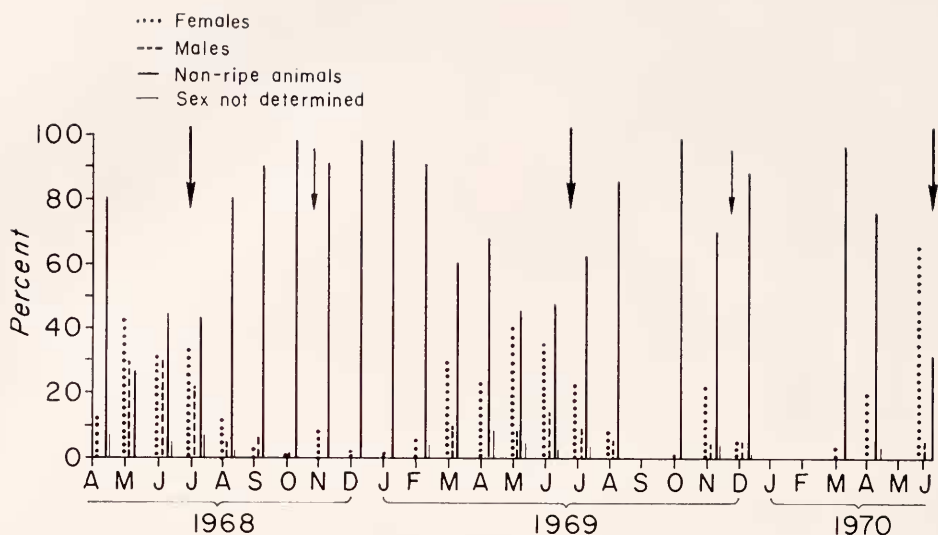


FIGURE 2. Per cent of the *Paranemertes peregrina* population at Snug Harbor comprised by males, females, and non-ripe animals each month. Large arrows indicate major spawning periods; small arrows indicate minor spawning periods.

ing was not observed in nature, the eggs of those that spawned in the laboratory did not form gelatinous masses. Extensive examination of all types of egg masses observed at both Snug Harbor and Garrison Bay showed none to be nemerteans. Single eggs of *P. peregrina* were also collected in the plankton of Mitchell and Garrison Bays in June, 1969. So, at least in the areas used for this study, *P. peregrina* spawns eggs and sperm into the sea.

Development. Eggs are yolky and about $235\ \mu$ in diameter; with the fertilization membrane and jelly coat, $650\ \mu$. They are blastulae in 30 hours. Larvae start swimming within the jelly case after about two days and hatch the third day when kept near 10°C . In two weeks the accessory stylets and basis rudiment of the proboscis have formed. There is continuous change from a ciliated tear-drop shaped, weakly swimming larva with two anterior flagella to an elongate, muscular, benthic form. Gradually, the tiny worm spends more and more time on the bottom until finally it cannot swim any longer. Larvae can stay in the plankton for at least eight weeks, but develop faster if food is available. The cultured worms started feeding in the laboratory on 3-segmented specimens of *Platynereis bicanaliculata* (about 0.2 mm long) when they were about one month old and less than 1 mm in length. Spionid larvae were also offered as possible food, but juvenile specimens of *P. peregrina* were never observed or induced to eat one. Although larvae were not specifically examined for food, those younger than about four weeks were never seen with any food material in the developing gut. It is assumed that they live on yolk reserves until they start feeding on polychaetes. Young specimens of *Nereis virens* quickly grew too large to be eaten by nemertean juveniles and showed the typical nereid swimming escape response to *P. peregrina* (Roe, 1970), even when the nemerteans were still in the flagellated swimming stage. Even as one-month old

TABLE I

Growth of three individuals of Paraneurtes peregrina in the laboratory.

Date	Size		Number of animals measured
	Area (1 × w, mm ²)	Length	
June 23, 1969	0.3 mm, egg diameter		3
August 11, 1969	—	0.15	1
August 21, 1969	—	0.4	1
October, 1969	<7, 6, <7	0.7, 1.1, 0.7	3
November, 1969	12.5, 13.5, 20	2.5, 2.7, 2.9	3
December 7, 1969	16.5–23.1, 36	3.3, 4, 3.3	3
December 17, 1969	41.6–46.8	5.2, 5.2	2
December 24, 1969	52, 54, 51	5.2, 5.4, 5.1	3
January 15, 1970	46.2, 52, 54	4.2, 5.2, 5.4	3
January 24, 1970	54.9, 58.2, 75	6.1, 6.5, 6.8	3
February 20, 1970	65–70	6.5–7	1*
February 27, 1970	112.5–120	7.5–8	1
March 8, 1970	120	8	1
March 22, 1970	ca. 135	9	1
April, 1970	ca. 180	12	1
May 24, 1970	285	15	1
June, 1970	310–350]	14–16	1**

* Largest of three young animals died February 8, 1970; it was already developing eggs when it died. One of the other two died in June, 1970; it quit feeding or growing in February, 1970, and became a ripe male.

** The third animal lived until December, 1970, at which time she spawned eggs and fragmented. In July, 1969, she pinched off part of her tail, so growth was not recorded thereafter.

worms less than 1 mm in length, *P. peregrina* has the strong food preference for nereids present in the adults; likewise, nereids show the escape response to *P. peregrina* throughout their lives. That the escape response is species-specific was reaffirmed when 3-segmented nereids showed aggressive rather than escape behavior toward a 2.5 mm specimen of *Zygonemertes virescens*.

Growth. In the laboratory three nemerteans were grown from eggs starting on June 23, 1969, until their deaths (Table I). They exhausted their food supply at the end of August and were not fed again until mid-October. Then they grew about 1 cm in length per month from October through March, 3 cm per month for the next two months, and then stopped. The sole survivor was 15 cm long at the end of a year (Table I). After the initial slow growth when they did not have food, the sizes of these laboratory-grown worms corresponded with the sizes of young in nature during the fall (Fig. 1A, September and 1B, December).

Adult nemerteans can also withstand periods of low food. The 14 nemerteans in the indoor artificial mud flat that contained no nereids generally lost weight and grew smaller each month, but one was still alive after nearly 7 months (October 1 to April 29). The average area decreased from 100 mm² for 14 worms in October to 58 mm² for 2 worms in December. Two worms collected in March averaged 74 mm²; they were probably among the largest animals in October. The average weight decreased from 109.3 mg in October to 68.7 mg in December. The two March worms averaged 89.2 mg (Roe, 1971 for details of each month).

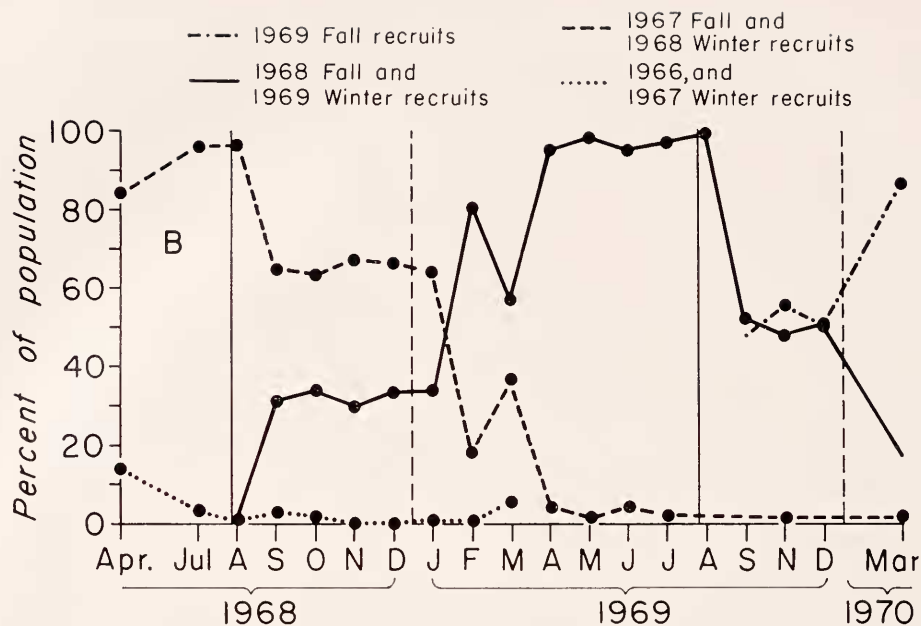


FIGURE 3. Per cent of Garrison Bay *Parancmeretes peregrina* population comprised by each year class. Vertical solid lines indicate periods of recruitment and increased density. Vertical dashed lines indicate periods of adult mortality.

Recruitment and age classes. Young worms produced at the peak spawning periods of April (Garrison Bay) and June (Snug Harbor) are apparent in the fall population. Worms produced during minor fall and winter spawning are easily seen in spring. Since the young are usually lighter in color than adults, the per cent of the population that is light-colored can be used as an estimate of recruitment. At Garrison Bay small light animals comprised 26% of the population in September, 1968, and about 22% in October, 1969. At Snug Harbor recognizable (small, light) young constituted 6.1 and 8.4 per cents for 1968 and 1969, but the Snug Harbor population also had many small, dark members. Since it was difficult to determine with certainty the ages of the small, dark worms, although in the same size classes as the recognizable pale young, these figures are probably low (see also Roe, 1971).

Juveniles gradually get darker as they grow, and by March or April it is difficult to distinguish them from adults of previous years. Figure 3 shows the proportion of the Garrison Bay population comprised by each year class, from study of nemertean growth rate in the laboratory and that of young nemerteans in nature (see also Roe, 1971).

Life span and mortality. If they survive larval settlement, almost all members of mud flat populations of *P. peregrina* live about 1.5 to 1.75 years. Worms produced in the spring probably reproduce the following spring; and those produced in winter, the following winter. If a worm spawns more than once, it is probably one that has outlived the average life span. Indeed, at Snug Harbor there is a

refuge near the -0.2 m tide mark where several large, old worms reside, and most worms 15 cm and longer seen in November–December were ripe. Light colored, small, young but ripe worms were also seen at Garrison Bay in the fall.

Mortality of *P. peregrina* was observed in nature only on very hot days when the lower low tide was just past noon; then only a few nemerteans were dying. Some animals also die after spawning. Size-frequency analyses (Fig. 1A, B) for the Garrison Bay population show sudden decreases in the numbers of large worms in fall or winter. Causes for these mortalities are not known. The gastropod *Aglaja diomedea* was observed to prey on *P. peregrina* (see also Gonor, 1964). However, *Algaia* is only large and common in summer when nemerteans are also large. Even the largest *A. diomedea* cannot eat an average sized adult *P. peregrina*; it can only bite off a piece of tail. *Aglaja* is also active at high tide, when the nemerteans remain underground. It is possible that *A. diomedea* has an effect on the numbers of small *P. peregrina* recruited, but it seems unlikely that it has much effect on the adult population. At Garrison Bay 2.7% of the *P. peregrina* population consists of worms with regenerating posterior ends; at Snug Harbor it is 5.1%, and at Edmonds, 3.5%. These percentages are biased downward, as regeneration was not always recorded, but the numbers of regenerating worms are few. *Aglaja* does not occur at Edmonds.

Another possible cause of mortality is parasitism by gregarines, although parasitized nemerteans appeared healthy. Twenty-six per cent of the Garrison Bay population had gregarine cysts in the faecal material. At Snug Harbor the average infection percentage determined from faecal analysis was 6.3%; and at Edmonds, 7.95%. In February, 1969, small pieces of gut tissue dissected from 17 Garrison Bay animals showed 88.2% were actually infected. Studies on the gregarine life cycle or on how nemerteans become infected were not done.

Population density. From numbers of nemerteans in twelve $\frac{1}{2}$ m² mud samples, it was estimated that 97% of the worms are active during the peak activity period of low tides in good weather during night tides at Garrison Bay. The total number/m² for Garrison Bay night tides is estimated per month as average density at low tide/0.97 (Fig. 4). In daytime summer low tides, ten samples of sieved mud yielded four inactive *P. peregrina*; two nemerteans were active in these areas. Because numbers were both low and variable, I was unable to determine with confidence the total number/m² for summer months. In spring, when lower low tides are in the afternoon, Garrison Bay nemerteans are not seen on the mud surface at low tide. By June, when these tides are in early morning, large (adult) worms are again seen in abundance (about 3/m²). It is concluded that the nemerteans remain under the surface in spring since animals in June are adult size (Fig. 1B) and since *P. peregrina* does not usually move great distances (see section below on movements).

At Snug Harbor 70% of the nemerteans seen during night low tides (14, $\frac{1}{2}$ m² samples) and 50% in daytime low tides (32, $\frac{1}{2}$ m² samples) were estimated to be active during peak activity periods of these tides, with total number/m² each month being the average density at low tide/0.7 (night tides) or /0.5 (day tides) (Fig. 5). The summer estimates of the percentage of active worms may be low, as mud was sieved on days when few worms were active. These irregularities should be

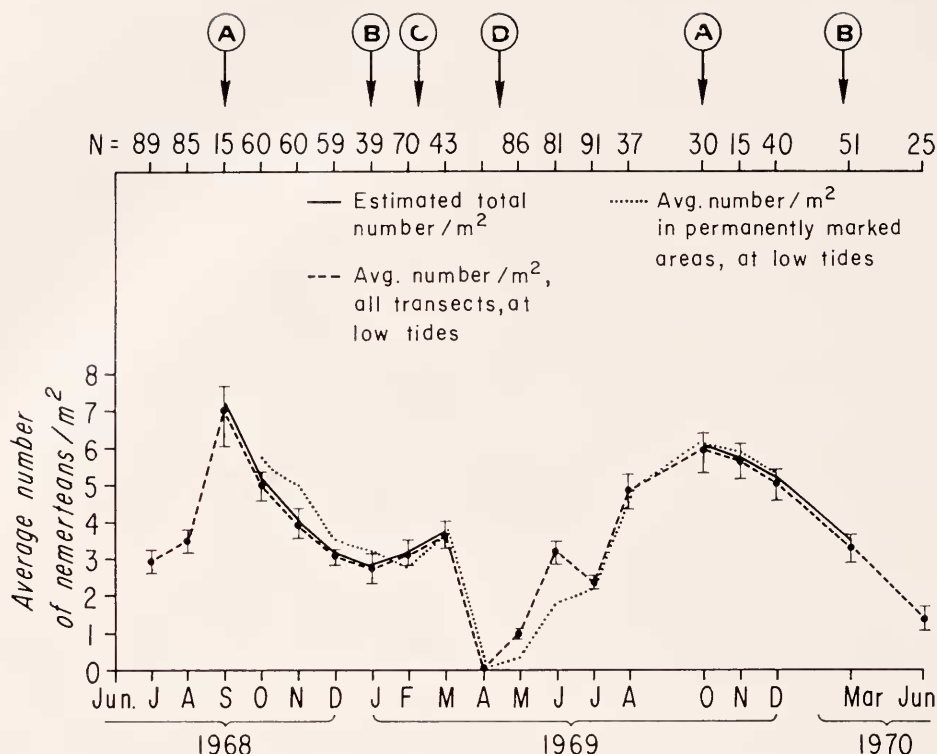


FIGURE 4. Mean densities (number/m²) of *Paranemertes peregrina* at Garrison Bay. A) shows fall recruitment of juveniles from eggs spawned the previous spring; B) major mortality period of adults; C) spring recruitment of juveniles from eggs spawned the previous fall; and D) low densities due to animals staying under the mud surface, not mortality. Vertical lines along dashed line are \pm one standard error from the mean. N is the number of 1 m² quadrats in which *Paranemertes* numbers were counted. Estimates of total density were calculated only for September 1968 to March 1969.

remembered during consideration of density information. At Edmonds only the numbers of active worms were counted (Roe, 1971).

At Garrison Bay (Fig. 4) and at Snug Harbor to some extent (Fig. 5) densities were highest in late summer and in fall, when both adults of the previous year and recruits from the previous spring or summer spawning seasons were present. Adults die in late winter (Fig. 3) reducing densities (Figs. 4, 5), but winter recruits add slightly to the populations then (Fig. 1A, B, small individuals seen in spring). At this time there is also replacement of the adult population by the present year's recruits, themselves reaching adult size (Fig. 1A, B).

Spring and summer are the most stable periods within each year with respect to density (Fig. 4); populations consists mainly of a one-year class (Fig. 5) and there is little mortality then. At Edmonds, such patterns were not determined. The number of active nemerteans depends strongly on weather conditions. Density measures in this higher intertidal area fluctuated too much for patterns to be

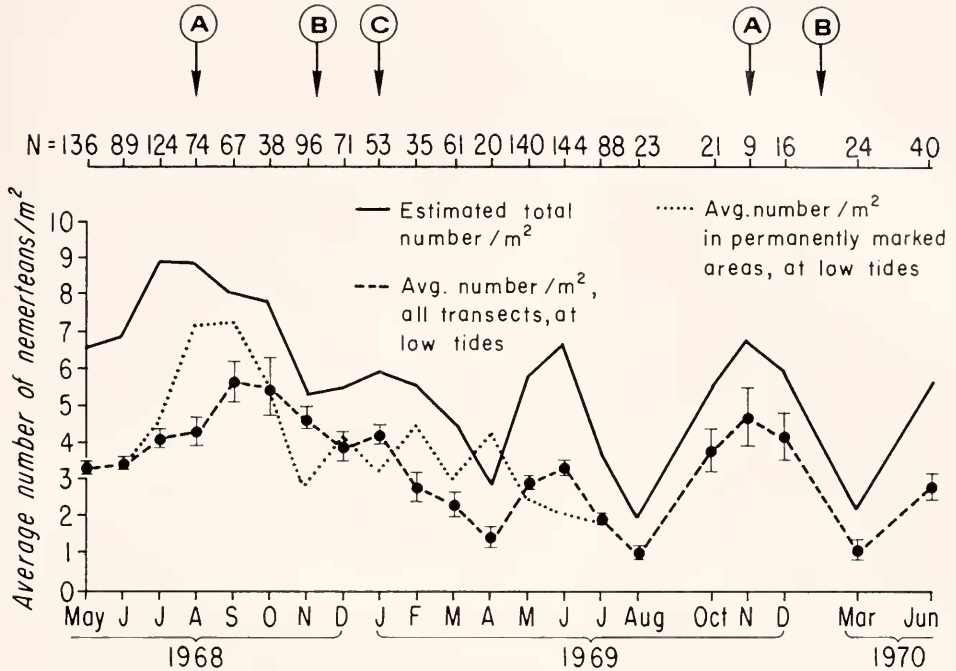


FIGURE 5. Mean densities (number/m²) of *Paranemertes peregrina* at Snug Harbor. A) shows fall recruitment of juveniles from eggs spawned the previous summer; B) major mortality period of adults; and C) spring recruitment from fall spawning. N is the number of 1 m² quadrats in which *Paranemertes* numbers were counted. Vertical lines along dashed lines are \pm one standard error from the mean.

seen. At Snug Harbor, life history and densities are similar to those at Garrison Bay (Figs. 2, 5; Roe, 1971) but show more fluctuations.

Prey densities

Platynereis bicanaliculata. An annual, *P. bicanaliculata*, has highly synchronous spawning periods. A few spawned in June, especially at Garrison Bay; but most of both the Snug Harbor and Garrison Bay populations spawned near August 1 in both 1968 and 1969, at which time there was almost a complete turn-over of each. Young specimens of *P. bicanaliculata* settle out of the plankton in about three weeks, 4 mm or less in length. They quickly grow to about 10 mm long, and overwinter at this size. In spring they grow to adult size (Figs. 6A, 7A; Roe, in preparation).

Since *P. bicanaliculata* is the major prey organism of both mud flat *P. peregrina* populations, densities of this species were most carefully and frequently determined. Figures 6B and 7B show densities through time. There are not such strikingly linear decreases in numbers at Snug Harbor as at Garrison Bay. When samples were divided into those with and those without algae, trends showed that *P. bicanaliculata* tends to be more abundant in algal covered areas than in bare mud,

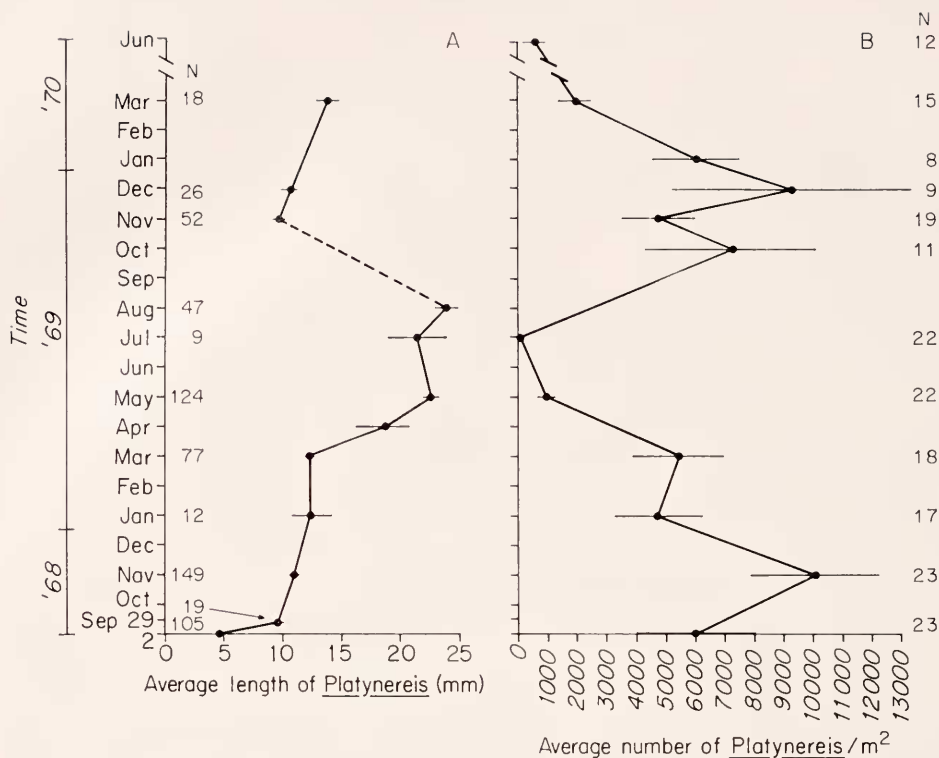


FIGURE 6. A) shows the average size \pm one standard error of *Platynereis bicanaliculata*, September, 1968 to March, 1970, at Snug Harbor. N is the number of worms measured; B) mean number \pm one standard error of *Platynereis bicanaliculata*/m² at Snug Harbor. The overall average number of *Platynereis* per m² is 3218. N is the number of samples taken. In August, 1969, young worms were collected and measured, but density was not determined.

although the numbers of samples in the two categories usually became too small to show significant differences (Roe, 1971). It was concluded that algal patchiness at Snug Harbor, not present at Garrison Bay, can account for the fluctuations. *P. bicanaliculata* is abundant in fall in both mud flats, with numbers decreasing until summer (Figs. 6B, 7B).

Other prey in mud flats. Densities of *Armandia brevis*, *Nereis virens*, and spionids were estimated from fewer samples than *Platynereis*; the estimates of average density thus do not reflect the patchy distribution of the three species. At Garrison Bay the average number/m² of spionids in 41 samples over four months was 76.5, the average number of *A. brevis* in 75 samples in seven months was 143, and the average number of *N. virens* in 49 samples in eight months was 3.3 (Roe, 1971 for data for each month). At Snug Harbor averages/m² were: *Scolelepis fuliginosa*, 119 in 87 samples over three months; *A. brevis*, 313 in 112 samples in seven months; *N. virens*, 21.5 in 46 samples over eight months. At Edmonds, densities were difficult to compare since large barnacles provide fewer (but larger) cracks to live in than do small ones, and different polychaetes occupy each type of

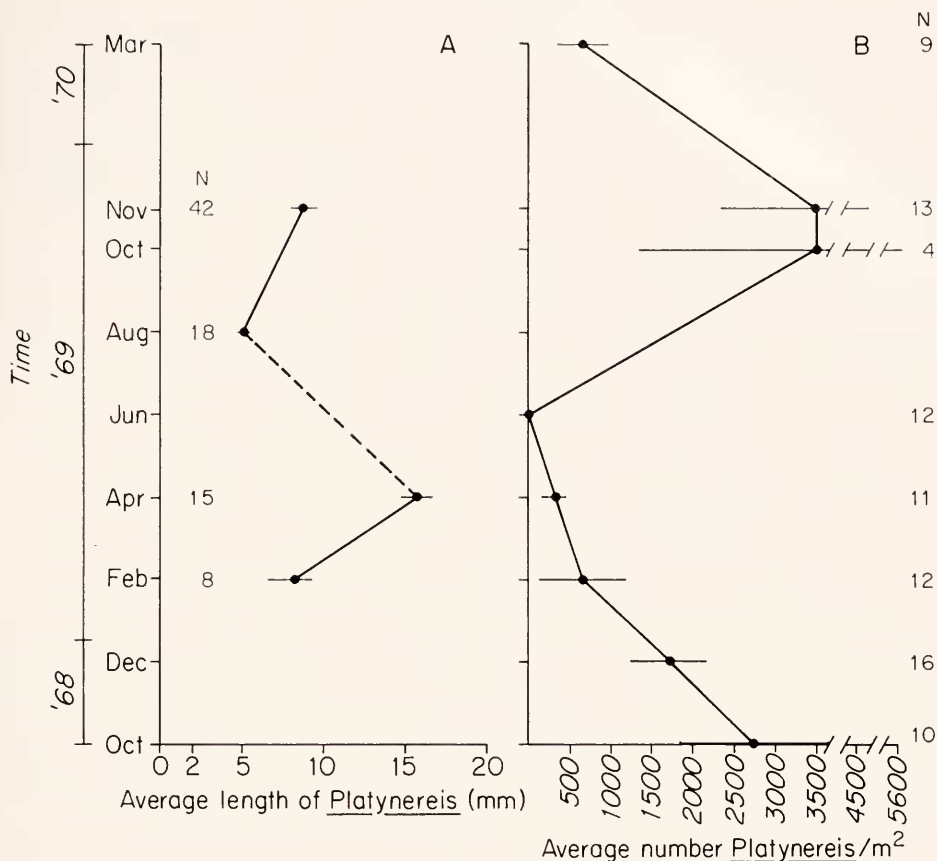


FIGURE 7. A) shows the average size \pm one standard error of *Platynereis bicanaliculata* February, 1969 to November, 1969, at Garrison Bay. N is the number of worms measured; B) mean number \pm one standard error of *Platynereis bicanaliculata*/m² at Garrison Bay, October, 1968 to March, 1970. N is the number of samples. All samples except June, 1968 (100 cm²) were 20 cm². Overall average number of *Platynereis*/m² is 815.6. In August, 1969, young nereids were collected and measured but density was not determined.

crack. Table II shows the number of prey/ml of barnacles and mussels. No polynoids were found in the barnacle and mussel samples for prey; however, 28 were eaten by specimens of *P. peregrina* in two years. Low densities of nereids are valid. Densities of *Paleanotus* are underestimates because they were not counted for several months and because they are difficult to see.

Feeding by *Paranemertes peregrina*

Feeding at low tide. *P. peregrina* is active soon after being exposed by the receding water during lower low tides: seeking out, capturing, and eating polychaetes.

Nemerteans were collected immediately after leaving their burrows as the receding tide uncovered the mud flat. Faeces of these worms were collected, as well as

TABLE II

Estimated number of prey/ml of barnacles and mussels at Edmonds.

Substratum	Prey	Samples			
		Number of samples	Volume of samples, ml	Number of prey collected	Average number per 1,000 ml substratum
Large barnacles	Syllids	10	10,125	222	21.9
	<i>Boccardia</i> sp.	9	9,625	200	20.8
	<i>Palcanotus chrysolepis</i>	2	950	5	5.3
	<i>Nereis vexillosa</i>	1	10,125	1	0.1
Medium sized barnacles	Syllids	4	1,950	43	22.1
	<i>Boccardia</i> sp.	4	1,950	311	159.5
	<i>Palcanotus chrysolepis</i>	1	250	12	48
	<i>Nereis vexillosa</i>	1	1,950	3	1.5
Small barnacles	Syllids	8	4,300	169	39.3
	<i>Boccardia</i> sp.	8	4,300	608	141.4
	<i>Palcanotus chrysolepis</i>	1	50	2	40
	<i>Platynereis bicaniculata</i>	1	4,300	1	0.2

faeces of worms collected about 1.5 hours after being uncovered by the receding tide, giving them time during the interval to feed. A significantly higher proportion of the latter had succeeded in feeding: at Snug Harbor, 28 had fed soon after being exposed, 120 had not; 96 had eaten and 77 had not after 1.5 hours exposure, $\chi^2 = 44.99$, $P < 0.005$. At Garrison Bay, five had fed and 21 had not soon after being exposed; seven had and 17 had not fed after 1.5 hours exposure, $\chi^2 = 0.660$, $0.5 < P < 0.25$. At Edmonds two had fed and 13 had not versus 15 feeding and 19 not feeding after 1.5 hours exposure, $\chi^2 = 4.35$, $P = 0.05$.

On the permanently marked areas at high tide periods when the substratum was under water, very few nemerteans were ever seen on the surface: an average of 0.01 worms was active/m² at Garrison Bay and an average of 0.03/m² was active at Snug Harbor. Even if these averages are multiplied by 23, the average number of hours the mud flats are under water per day, densities are only 0.23 and 0.69 worm/m², far lower than low tide densities (Figs. 4, 5). No worms were seen while diving at Edmonds. The nemerteans could be burrowing beneath the mud and capturing food, but in light of their "homing" behavior (see below), it is thought that they move little, unless disturbed, between exposure at low tides.

The artificial mud flat, run for ten months without "low tides," showed that the 16 nemerteans in the experiment shrank. One large worm decreased from 570 mg weight and 475 mm² in area to 226 mg and 142.5 mm² from October to April; a second decreased from 638 mg and 388.5 mm² to 283.5 mm² from October to March (not weighed in March). One group of smaller nemerteans decreased from average weights of 140 mg and average areas of 135 mm² between October and August to 35 mg and 44.2 mm². A second group decreased from average weights of 125 mg and average areas of 115 mm² to 36.3 mm² (not weighed) between October and August (Roe, 1971 for details). This decrease in size can be at-

tributed to decreased feeding when there are no low tides, since many nereids were added to the aquarium periodically. However, *P. peregrina* has been observed feeding under water. It was concluded that in nature *P. peregrina* feeds primarily when exposed at low tide, although feeding can occur at other times, as in September and March, when few tides are low enough to expose the nemerteans.

Length of activity period. Many nemerteans are active during the first two hours after the tide recedes during months with daylight low tides, and during the first 2.5 hours in night low tides. Average density of active *P. peregrina* soon after the worms were exposed by the receding water during daylight tides was $3.3/\text{m}^2$, and after 1.5 hours, $1/\text{m}^2$; at night in 1.5 hours, densities decreased from $4.5/\text{m}^2$ to $2.8/\text{m}^2$. (Counts were made in the same square meters earlier and later.) Activity is modified considerably by weather. Rain, snow, and strong afternoon sun reduce the numbers of worms out and the length of time any one worm stays out. At Snug Harbor (one night in November) density was $3.9/\text{m}^2$ before it started raining, $1.4/\text{m}^2$ shortly after; density at Garrison Bay in March was $4.1/\text{m}^2$ after dark, and only two nemerteans were seen on the whole mud flat during two afternoon low tides. March night tide and afternoon densities at Snug Harbor were 3.2 and $0.8/\text{m}^2$, respectively.

Movements. Recaptures of 48 nemerteans dyed with neutral red and put into three marked 1 m^2 areas in September, 1968 at Garrison Bay showed: October, 32 recaptured, 67%; November, 12 recaptured, 25%; December, 5 recaptured, 10.4%; January, 2 recaptured, 4.2%; February, 1 recaptured, 2%; April, 1 recaptured, 2%; May, 1 recaptured, 2%.

At Snug Harbor 14 red nemerteans were put into a 1 m^2 plot in July, 1968. Results were: August, 6 recaptured, 42.9%; September, 2 recaptured, 14.3%; October, 1 recaptured, 7%; November, 1 recaptured, 7%.

Forty-nine red nemerteans were put into seven different marked 1 m^2 areas along a transect at Snug Harbor in September, 1968. Of these, 12 were recovered in five areas after one month; six were recovered in five areas after two months; two in two areas after three months; and four worms were collected in four respective square meters after five months. After five months, 4 out of 49 animals were still in the same meter where they had been placed.

After two weeks, experimental areas at Snug Harbor cleared of nemerteans had approximately 50% as many worms as before. Clearing experiments suggest that nemerteans will move into empty areas rather quickly. However, on several occasions it was casually noted that nemerteans stayed active longer and crawled more where many bootprints were left in the mud. Clearing an area disturbed not only that area but also the ground around it, perhaps causing worms in those areas to be more active than normal.

From Pielou, 1959, it is seen that when *P. peregrina* is active at low tide, individuals are randomly dispersed: at Snug Harbor the probability of random dispersion was $\gg 0.05$ in October, 1968; > 0.05 in November, 1968; > 0.05 in June, 1970 and in a second sample in June, 1970, $\gg 0.05$. At Garrison Bay the probability of random dispersion was $\gg 0.05$ in July, 1969 (see also Roe, 1971).

Individual feeding behavior. Feeding behavior of individual worms was observed both in nature and in artificial mud flats. The following is a synthesis of many observations. When the tide recedes at the beginning of a low tide period, the

nemerteans emerge from their burrows and search for food. Most worms are out about 15 minutes after the water leaves an area (average time in 30 laboratory observations, 13.9 minutes). In the artificial mud flats (18 observations) worms crawled an average of 30 cm in 18 minutes in search of food. There is much variation in the distances traveled and speed of crawling.

P. peregrina searches haphazardly until it comes upon a nereid or a fresh nereid trail or tube. When contact is made with a trail it crawls along the trail, not always in the same direction as the nereid. It frequently loses the prey even if it comes upon the prey itself. The swimming-flipping escape response of nereids (Roe, 1970) is quite effective; contact with the nereid causes a flurry of motion, destroys the trail, and the nemertean sometimes loses the prey. *P. peregrina* was observed a few times to lift its head, swinging it back and forth across a trail. This behavior suggests that close-range chemoreception helps keep the nemertean oriented. *P. peregrina* has no distance chemoreception to aid in prey detection; it must bump into the prey or immediate surroundings of the prey with its head before it recognizes prey as prey. In the artificial mud flats *P. peregrina* spent an average of 17.8 minutes in random crawling before finding a nereid trail, tube, or nereid, and another 23.7 minutes poking its head down worm tubes and chasing prey organisms, for a total search time of 41.5 minutes. Search time was terminated when the feeding process (Roe, 1970) started or when a nemertean started home, having found no food.

When prey is found, feeding takes only a few minutes. In the artificial mud flats average feeding time was 8.3 minutes; in nature, 7.3 minutes. It takes longer if a *P. peregrina* goes into a *P. bicanaliculata* tube to feed, and it takes much longer (over an hour) if one tries to eat a nereid much larger than itself.

P. peregrina seems able to eat only polychaetes that are at or very near the surface of the mud or those that have broad tubes. Maldanids, oweniids, lumbrinerids, and other abundant polychaetes having deep, vertical tubes with small diameters were not eaten by the nemertean.

After feeding, *P. peregrina* usually backs up a few centimeters along the mucus trail it made during the search for food; then it turns around and crawls on the trail until it reaches its burrow, where the nemertean disappears underground. Most individuals return to their former burrows after each meal; they only make new burrows if part of the mucus trail was destroyed and they cannot find their way home.

The total time spent out at low tide looking for food, eating, and returning home averaged 41 minutes in the artificial mud flats and 43 minutes in nature for individual worms (not always the same observations as studied for crawling and searching).

Prey species and diversity of diet. Food preference experiments (Roe, 1970) indicated that behaviorally *P. peregrina* prefers to eat nereids over other polychaetes. (In this paper the word *preference* refers to what animals ate most often when given choices in laboratory experiments of Roe, 1970. The word *selectivity* refers to what animals actually eat in nature.) Faecal analysis of worms in nature also showed that nereids are the major prey in areas where they are available (Table III).

Specimens of *P. peregrina* at both Snug Harbor and Garrison Bay mainly eat nereids throughout the year (Fig. 8; Roe, 1971). In all three populations there is

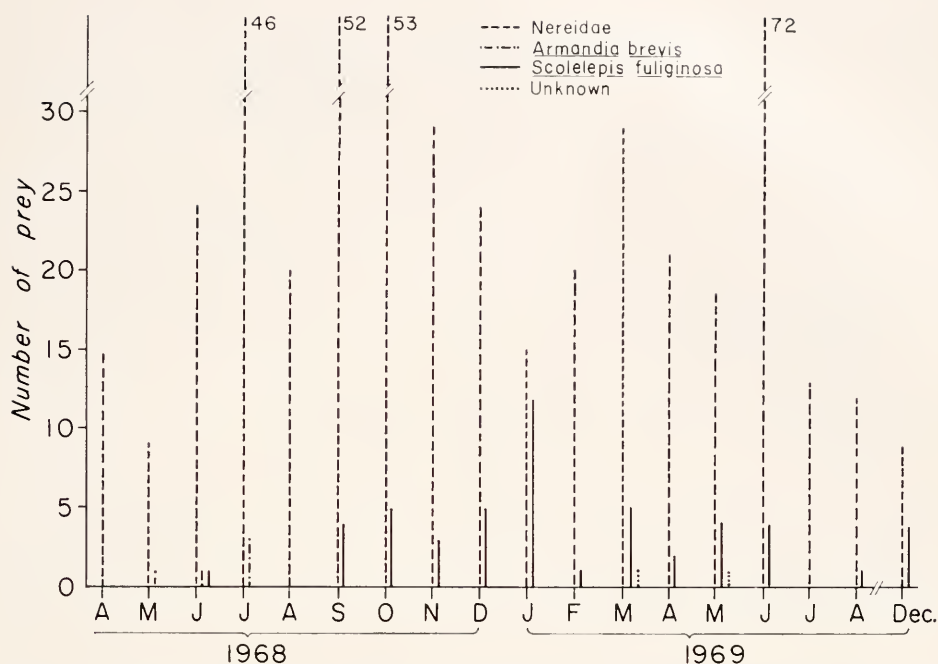


FIGURE 8. Numbers of each prey eaten by Snug Harbor *Paramermertes peregrina*, April, 1968 to December, 1969.

a significant increase in feeding on spionids during the winter: at Snug Harbor between September and April they ate 39 spionids, 234 other prey; between May and August they ate 12 spionids, 257 other prey; $\chi^2 = 15.34$, $P < 0.005$. At

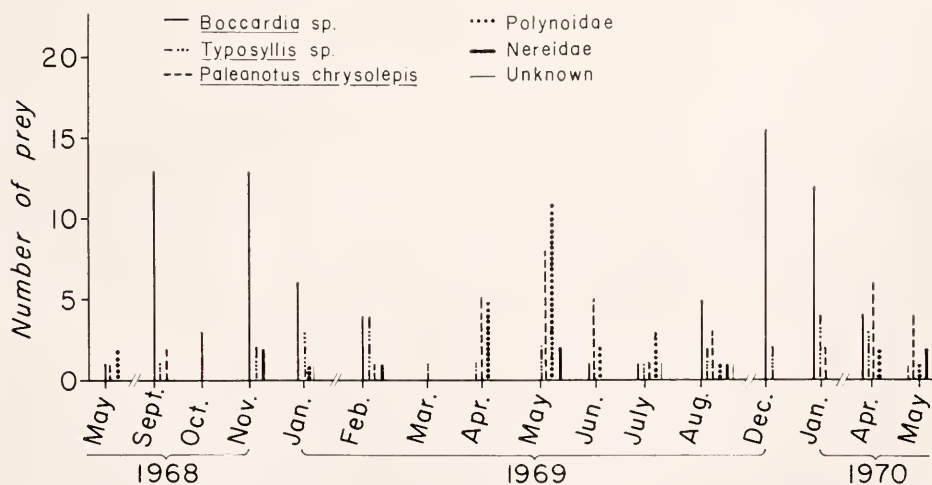


FIGURE 9. Numbers of each prey eaten by Edmonds *Paramermertes peregrina*, May, 1968 to May, 1970.

TABLE III
Per cent of total diet comprised by each prey species.

Prey species	Snug Harbor	Garrison Bay	Edmonds
<i>Platynereis bicanaliculata</i>	80.0	68.4	1.6
<i>Nereis vexillosa</i>	2.6	3.5	2.7
Nereids*	6.7	4.1	
Total Nereidae	89.3	76.0	4.3
Spinoids	9.4	18.1	43.1
<i>Ophiodromus pugettensis</i>	0	5.1	0
<i>Armandia brevis</i>	0.9	0.9**	0
<i>Paleanotus chrysolepis</i>	0	0	20.8
Polynoids	0	0	15.3
<i>Typosyllis</i>	0	0	14.7
Unknown*	0.4	0	1.6
Total	100.0	100.1	99.8
Total number prey	542	216	183

* In these samples there were too few setae or some other reason which made species identification unreliable.

** These setae were tentatively identified as *Armandia*; they might conservatively be placed under "unknowns."

Garrison Bay between October and February they ate 31 spionids and 80 other prey; between March and September, 6 spionids, and 91 other prey; $\chi^2 = 16.73$, $P < 0.005$. At Edmonds between September and February they ate 67 spionids and 27 other prey; between March and August they ate 12 spionids and 78 other prey; $\chi^2 = 62.99$, $P < 0.005$.

Small numbers of *Armandia* and *Ophiodromus pugettensis* are also eaten at Snug Harbor and Garrison Bay, especially in summer (Fig. 8; Table III). At Edmonds *Paleanotus* and polynoids replace spionids as the major prey during summer. Syllids (*Typosyllis* sp.) are eaten throughout the year (Fig. 9; Table III) at Edmonds.

Using Pielou's (1966) diversity index, it was found that at Edmonds, prey-species diversity is significantly higher in summer ($H' = 1.39 \pm 0.02$) than in winter ($H' = 0.89 \pm 0.04$) at the 95% level. At Garrison Bay prey-species diversity is essentially the same in summer ($H' = 0.66$) and in winter ($H' = 0.64$). At Snug Harbor summer months show a significantly lower diversity ($H' = 0.30 \pm 0.01$) than winter months when many spionids are eaten ($H' = 0.44 \pm 0.03$) at the 95% level. Prey-species diversity is higher at Edmonds than at Garrison Bay and higher at Garrison Bay than at Snug Harbor.

Electivity. Electivity coefficients (Ivlev, 1961) of all prey species whose relative densities in nature are known indicate that at Snug Harbor and Garrison Bay specimens of *P. peregrina* eat nereids about as often as they come into contact with them (electivity coefficient for Snug Harbor, +0.01; for Garrison Bay, +0.10), that they select spinoids (+0.70 and +0.51), and that *Armandia* is usually passed by (-0.81 and -0.85). At Garrison Bay *Ophiodromus* is also usually passed by (-0.61). Actually, nereids are probably sought out soon after *P. pere-*

grina is uncovered by the receding water of low tide when the nemerteans are hungry but are more likely than other species to be passed up later in the low tide period when the nemerteans have already fed, simply because nereids are so much more abundant than other species.

At Edmonds, *Palcanotus* (+0.16) and nereids (+0.87) are selected, *Typosyllis* (-0.24) is not, and *Boccardia* is eaten as it is encountered in winter (-0.005) and in cracks between small barnacles where it is very common (-0.01) and is eaten less often than encountered in cracks of large barnacles (-0.32). The high electivity for *Palcanotus* is probably a function of underestimating *Palcanotus* densities. Four feeding experiments suggested that *Paranemertes* will not often accept *Palcanotus*.

Natural history and escape responses. Although electivity shows mathematically what prey *P. peregrina* selects, this coefficient is not nearly sufficient to explain feeding patterns. Behaviorally, *P. peregrina* strongly prefers nereids to all other prey (Roe, 1970), yet electivity values of mud flat populations indicate little selectivity. Natural history of prey, and prey behaviors, as escape responses, are important in determining prey availability. Densities alone are insufficient for understanding availability.

At Snug Harbor during low tides on hot summer days specimens of *P. peregrina* were feeding almost exclusively on *Armandia brevis*. (In all observations on feeding 21 specimens of *A. brevis* were seen being eaten, plus four attempts by nemerteans to eat *Armandia*.) However, *A. brevis* is less than 1% of the nemertean diet there (Table III). *A. brevis*, a normally active animal, has a highly effective flipping, swimming escape response to touch. Only on hot summer days when the low tide is in early afternoon can *P. peregrina* catch *Armandia*, sluggish from heat stress. Availability of this prey is, therefore, temporally highly patchy.

At Garrison Bay *P. peregrina* caught and ate juvenile *Ophiodromus* in summer. *Ophiodromus* as an adult makes *P. peregrina* turn another direction upon contact and not even attempt to eat it. Juveniles are only present in summer.

P. peregrina tries to feed on *Nereis virellosa* about as frequently as on *Platynereis*. However, faecal analysis shows that *N. virellosa* comprises only 2.6% of the food actually eaten versus 80% being *Platynereis* (Table III, Snug Harbor). Food preference tests (Roe, 1970) showed that it is harder for the nemerteans to finish the feeding process with *N. virellosa* as prey. Present studies confirm this; over half of the observations on feeding in nature were not completed (*P. peregrina* ate nine nereids but did not complete feeding on 11 others in 20 observations). *N. virellosa* has several escape mechanisms making it less available. It escapes in size from *P. peregrina* twice in its life span. When tiny (3 to 8 segments), it is potential prey for one to two month old nemerteans only; adult nemerteans do not notice prey this small. However, it quickly grows to a size that the slower growing young nemerteans cannot handle. During the first year of the nereid's life span, after it reaches a size to be noticed by larger nemerteans, it is a size that *P. peregrina* can eat. In the second year (Roe, in preparation) the nereids grow too large in diameter for the nemerteans to ingest. These large nereids also usually recover from the paralytic effects of the toxin injected into them during unsuccessful attempts by *P. peregrina* to feed on them. *N. virellosa* also displays the typical swimming escape response of nereids to *P. peregrina* (see Roe, 1970). This escape response is in effect throughout life; a three-segment *Nereis* showed response to touch by a

larval *Paranemertes* 0.3 mm in length. Large nereids show aggressive behavior toward specimens of *P. peregrina*; instead of just trying to escape, they sometimes bite their attackers. If a nereid bites a nemertean's proboscis, the nemertean cannot draw the proboscis back within its rhynchocoel, and feeding, if successful at all, takes much time. Finally, *N. texillosa* tends to become active at the end of a low tide period when water is beginning to cover the mud. As this is the time when nemerteans have already fed and are returning home, the nereid activity period becomes a protective device.

Platynereis bicanaliculata is the major prey of *P. peregrina* where it is common. It is in the preferred food family, and it has only the flipping-swimming escape response. This behavior is much more effective at high tide, and *P. peregrina* usually succeeds in capturing *Platynereis* at low tide. It is suggested that *P. peregrina* has evolved to do most feeding when low tides expose the substratum because the nereid escape response is less effective when the nereid can only flip a few centimeters than when it can swim away. *P. bicanaliculata* is of a size range suitable for eating throughout the year (Figs. 6A, 7A). It was never observed to fight back when struck by a nemertean. Syllids are difficult for *P. peregrina* to ingest even though they are small (Roe, 1970).

The difference in feeding in all three populations on spionids in winter and summer must be due in part to behavioral differences that make spionids more available in winter. Densities of spionids are roughly the same in both seasons (my observations for Snug Harbor, confirmed by S. A. Woodin, Johns Hopkins University, in personal communication), and nemerteans strongly preferred nereids in food preference tests run during winter (Roe, 1970).

Time taken for passage of food through the gut. Defecation usually occurs 18–20 hours after feeding (see also, Roe, 1970; Gibson, 1970), so faecal samples obtained from worms of a given tidal period represent feeding that occurred during that same tide.

Feeding time through a tide series. Worms were collected every day over four to six days, when lower low water level uncovered them; presence or absence of faeces of worms collected on early or on later days during a low tide series showed no significant differences in numbers of worms feeding at the beginning and at the end of the tide series (Snug Harbor: days 1–2, 19 fed, 69 did not; days 5–6, 9 fed, 45 did not; $\chi^2 = 0.512$. Edmonds: days 1–2, 7 fed, 11 did not; days 3–4, 8 fed, 11 did not; $\chi^2 = 0.037$). It was concluded that in general *P. peregrina* feeds about every day if it can find prey.

Feeding per cents through the year. At Snug Harbor an average of 66.5% of the population ate per low tide during night low tides (September to January, 149 of 224 worms collected had eaten). During daylight low tides of April to July an average of 33.1% ate during a low tide (199 of 401 worms collected). At Garrison Bay during night low tides of September to January an average of 44.5% (85 of 191 collected) ate per low tide. In daylight tides of April to July an average of only 16.4% (46 of 279 collected) ate per low tide. At Edmonds daytime and night patterns were less striking; the overall feeding rate was 38.6% (183 of 474 worms collected). (See Roe, 1971, for details for all 3 populations.)

Since nereids have jaws, the number of prey eaten per nemertean can be determined from faecal analysis. At Snug Harbor during night low tides of September

to March an average of 19.7% (42 of 213 worms collected), and during daylight tides of April to August 12.3% (19 of 155) of the nemerteans which had fed had eaten more than one prey item while exposed at a given low tide. At Garrison Bay during night tides of August to March an average of 11.4% (16 of 141 collected), and during daylight tides of April to July, none of the feedings were multiple. Comparable data are unavailable for the Edmonds population since few prey had markers to distinguish between two similar-sized prey of the same species.

Maximum feedings rate. From laboratory feeding experiments in which 12 nemerteans were fed as many individuals of *P. bicanaliculata* as they would eat per day (experiments lasted varying lengths of time) and information derived from the numbers of nereids eaten per day by the three juveniles grown in the laboratory for 6–18 months, it was determined that an individual *P. peregrina* eats 0.83 to 0.95 polychaete per day, if prey is available.

Size of prey eaten. More detailed studies of feeding on *P. bicanaliculata* were done since prey sizes could be determined by measuring jaws in faeces. A linear regression of nereid length to jaw length is significant (length = 31.9 jaw length - 5, $F = 249.27$, $P < 0.005$). During most of the year there was no significant correlation or linear regression between nemertean size and the size of *P. bicanaliculata* eaten. Data were divided into seasons corresponding to the three size categories of *P. bicanaliculata* (Fig. 6A). Results show: late August to early September, $r = 0.803$, $N = 12$, $P = 0.001$; October to March, $r = 0.201$, $N = 72$, $0.1 > P > 0.05$; April to July, $r = 0.084$, $N = 67$, $P > 0.1$. In August a few large individuals of *P. bicanaliculata* are still available as food, and new recruits are small enough (about 4 mm long) to escape notice of larger nemerteans. So for a brief time, one sees large nemerteans usually eating last year's adult prey and nemertean recruits eating nereid recruits. But, by early October, no adults of *P. bicanaliculata* remain and recruits have grown large enough (10–12 mm, Fig. 6A) for all nemerteans to eat.

P. peregrina tended to eat more of the larger prey than the smaller ones during fall and winter when nereids are generally small. Significant differences between sizes eaten and sizes available were determined using Student's *t*-test, with the following results: early September, 1968, $t = 2.309$, $0.05 > P > 0.025$; late September, 1968, $t = 0.190$, $0.10 > P > 0.05$; November, 1968, $t = 2.222$, $0.05 > P > 0.025$; January, 1969, $t = 1.742$, $0.10 > P > 0.05$; March, 1969, $t = 3.518$, $0.001 > P$; April, 1969, $t = 0.848$, $0.5 > P > 0.4$; May, 1969, $t = 1.306$, $0.2 > P > 0.1$; December, 1969, $t = 1.123$, $0.3 > P > 0.2$.

Individuals of *P. peregrina* that had eaten more than one prey during a low tide were not significantly larger than those that had eaten only one prey. *T*-tests of the two groups of nemerteans gave the following results: late August to early September (a 2–3 week period), $t = 0.60$, $0.6 > P > 0.5$; late September to March, $t = 0.35$, $0.8 > P > 0.7$; April to early August, $t = 0.02$, $0.9 > P > 0.8$.

The average size of *P. bicanaliculata* eaten in multiple feedings was not significantly different from the average size eaten in single feedings. Jaw sizes of nereids from multiple feedings and from single feedings were compared using *t*-tests: late August to early September (a 2–3 week period), $t = 1.17$, $0.3 > P > 0.2$; late September to March, $t = 0.834$, $0.5 > P > 0.4$; April to early August, $t = 1.75$, $0.1 > P > 0.05$.

TABLE IV

Estimated number of each species eaten by Paranemertes peregrina per square meter per year and per cent of each population consumed.

	Snug Harbor		Garrison Bay		Edmonds*	
	Number	Per cent	Number	Per cent	Number	Per cent
<i>Platynereis bicanaliculata</i>	437.2	13.6	281.2	34.5	9.6	83.5
<i>Nereis vexillosa</i>	14.3	65.0	14.4	436.4	16.0	96.4
Nereid sp.	36.4	—	16.8	—	—	—
Total Nereidae	488	15.1	312.4	38.1	25.6	91.9
Spionidae	51.5	43.3	74.2	96.0	252.2	24.3** 3.2*** 3.6****
<i>Armandia brevis</i>	5.0	1.6	3.8	2.7	—	—
<i>Ophiodromus pugettensis</i>	—	—	20.9	—	—	—
Syllidae	—	—	—	—	86	7.9** 7.8*** 4.4****
<i>Palaeonotus chrysolepis</i>	—	—	—	—	121.5	—
Polynoidae	—	—	—	—	89.5	—

* Numbers/1,000 ml were multiplied by 50 to get an estimate of numbers/m².

** In samples of large barnacles.

*** In samples of medium-sized barnacles.

**** In samples of small barnacles.

Estimated number of prey eaten by P. peregrina. The direct effect of *P. peregrina* on prey species is to reduce their numbers. The estimate of the average number of prey eaten by specimens of *P. peregrina* per m² per year was calculated to be 546.5 at Snug Harbor and 411.1 at Garrison Bay. At Edmonds the minimum estimate (585.1 prey/m²/yr) was considered most correct (see Roe, 1971, for details and methods of calculating these figures). Table IV shows the number of individuals of each species eaten per year per m² and what per cent of the available prey population is eaten by the nemerteans per year. These figures are reliable for all specimens of *P. bicanaliculata*, *N. vexillosa* at Snug Harbor, and spionids and syllids at Edmonds. Densities of spionids at Snug Harbor and *Armandia* at Snug Harbor and Garrison Bay are probably fairly correct.

DISCUSSION

Although life histories of two populations of this nemertean were similar, spawning periods were different in all three populations. Spawning must be associated with local events. Larvae of *P. peregrina* can survive at least eight weeks without food, or they can start feeding within a month after being spawned. One month old nemerteans indicated that they, like adults, show a strong preference for nereid prey. *N. vexillosa* spawns from March through August (Roe, in preparation), but the egg masses are patchily distributed and the three-segmented young quickly outgrow very young specimens of *P. peregrina*. *P. bicanaliculata* is probably the main food

source for very young nemerteans; it is temporally predictable and abundant. The timing of nemertean spawning has probably evolved to coincide closely enough with its major prey's spawning that the tiny nemerteans find food sometime within their first two months of life. Some individuals of *P. bicanaliculata* spawned in late June at Garrison Bay, whereas nearly all at Snug Harbor did not spawn until August; nemerteans spawn later at Snug Harbor than at Garrison Bay. Spionid larvae are in the plankton throughout spring and summer and might also be a food source, especially for the young at Edmonds.

Feeding is a most important activity for any animal. For predators that pursue relatively large prey, the most adaptive strategy is to specialize when food is abundant but become less specialized when food becomes scarce (Enlen, 1966; MacArthur and Pianka, 1966; Ivlev, 1961).

P. peregrina is a pursuer, spending on average 18 minutes haphazardly searching for prey, and 24 more minutes in pursuit of prey or in poking its head down prey tubes.

This study of *P. peregrina* allowed predator strategy theories to be tested by comparing behavior of the same species in areas varying greatly in abundance of preferred nereid food. Snug Harbor had an average of 3240 nereids/m², Garrison Bay, 819/m², and Edmonds, about 28/m² (Figs. 6B, 7B; Table II). At Snug Harbor the preferred nereids constituted 89% of the diet, and there were two minor prey. At Garrison Bay nereids comprised 76% of the diet, and there were three minor prey groups. Spionids were relatively more important, comprising 18% of the total. And, at Edmonds, nereids comprised only 4.4% of the diet, with spionids increasing to 43% and diversity of prey increasing to five families (Table III).

At Snug Harbor a higher proportion of the nemerteans fed during low tide periods (overall feeding average of 42.8%), and a greater number of nemerteans ate more than one prey per low tide period (overall average of 16.9%) than at Garrison Bay (overall average feeding of 30.5%) with 9.6% being multiple feedings over the year. At Edmonds 38.6% of the nemerteans sampled during low tide periods had fed. From the proportion of nemerteans feeding, Snug Harbor appears to be the best of the three areas for *P. peregrina*. And, although prey are abundant at Edmonds, preferred prey are not; adult nemerteans there are far smaller than adults at either mud flat areas (Fig. 1A, B; Roe, 1971). It appears that the preference *P. peregrina* shows for nereids reflects a long evolutionary association with these prey with a correlated greater efficiency in capturing or assimilating them to other species. The Edmonds population may be food-limited in spite of a seeming prey abundance.

Seasonal feeding patterns exist within each population. At Snug Harbor prey-species diversity is significantly higher from September to March than April to August. This appears contradictory to prediction, as *P. bicanaliculata* averages 6000/m² in winter and only 260/m² in summer (Fig. 6B), and the per cent of *P. peregrina* feeding per low tide period in winter was greater (67%) than in summer (33%). However, *P. bicanaliculata* individuals are two to three times as large in linear dimensions in summer as in winter, and some are ripe females; both factors enhance the food energy per prey individual consumed in summer. Since all three populations of nemerteans did eat spionids in fall and winter, it appears that *P. peregrina* is to a limited extent an opportunist. Another suggestion of

opportunism is the observation that *Armandia* was eaten in large numbers when the *Armandia* individuals were sluggish. *P. peregrina* may consume a less abundant, less preferred food in spite of an abundance of preferred nereids if the less preferred food becomes easily available.

The direct effects of predators on their communities are those they have on their prey populations (e.g., Connell, 1961, 1970). Indirect effects are observed when changes in prey populations cause further alterations in community structure, changing abundances and diversity among organisms not directly affected by the predator (e.g., Paine, 1966; Dayton, 1971).

Direct effects of *P. peregrina* are in lowering prey densities and in lowering reproductive potentials of prey species. From estimates of the feeding rate of *P. peregrina* and of prey densities, it was found that on mud flats *P. peregrina* eats 14–35% of the standing crop of *P. bicanaliculata* per year (Table IV). At Snug Harbor *P. bicanaliculata* is so numerous this 14% probably has little effect on reproductive capacity. At Garrison Bay, where nemerteans crop 35% per year, few nereids reach maturity; and even though each surviving female released thousands of eggs, recruitment was considerably lower than at Snug Harbor (Figs. 6B, 7B).

Whether *P. peregrina* has important indirect effects on its communities is a function of its prey; it is only when the major prey is the superior competitor for a basic resource that indirect effects of predation are strongly felt throughout the community (Paine, 1969).

At Snug Harbor, *P. bicanaliculata* is a major holder of the limited space available (Woodin, 1974). Significant reduction of nereid numbers allows larger numbers of *Armandia* and *Axirothella* (maldanid) to survive (Woodin, 1974). By heavy predation on *P. bicanaliculata*, *P. peregrina* can help maintain densities of other polychaetes in its communities. At Garrison Bay polychaete diversity is higher than that at Snug Harbor; this may in part be a result of the nemertean's cropping more of the nereid population there.

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SUMMARY

In Washington State, *Paranemertes peregrina* spawns in spring and summer, with minor spawning periods in fall. Juveniles from spring spawning are first easily seen the following fall, when the population consists of both adults and juveniles. Throughout winter adults die and juveniles mature, becoming ripe for the spring and summer spawnings. These adults die the following winter; the life span is thus 1.5 to 1.75 years.

P. peregrina feeds exclusively on polychaetes; at both mud flats *Platynereis bicanaliculata*, an annual, was abundant and the dominant prey organism.

Observations in nature and in artificial tidal flats constructed in the laboratory permitted study of foraging behavior and activity patterns. *P. peregrina* emerges from its burrow when exposed by the receding tide and searches haphazardly until it contacts acceptable prey. After contact, feeding takes seven to eight minutes. Then *P. peregrina* returns to its burrow by following its own mucus trail. Individuals often remain within a one meter radius for several months. Maximum feeding rate was determined in laboratory studies to be 0.8–0.95 prey individual per day.

In two intertidal mud flats and one rocky area, testing of predator strategy models and effects of predation on prey populations showed that in all three areas the percentages of nereids in the diets of *P. peregrina* were directly proportional to nereid density. Prey-species diversity was inversely proportional to nereid density. *P. peregrina* ate a significantly greater number of spionids during fall and winter than during spring and summer. *Armandia brevis* was also eaten by mud flat populations in summer, as was *Ophiodromus pugettensis* in one area. Polychaetes of five families comprised the diet of the nemerteans in the rocky area. Escape responses strongly affect prey availability. On mud flats *P. peregrina* tends to select *P. bicanaliculata* larger than the mean size available during fall and winter when *P. bicanaliculata* is small; larger nemerteans do not select larger prey than do small ones.

P. peregrina crops 14–35% of the *P. bicanaliculata* population per year, and probably somewhat higher proportions of *Nereis virens* and spionid populations. At the location where predation on nereids was more intense, their recruitments were lower. By heavy predation on *Platynereis*, *P. peregrina* may help maintain densities of other polychaetes in its communities.

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